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A COMPUTER SIMULATION MODEL
OF SEASONAL VARIATIONS IN OCEAN PRODUCTION
FOR A REGION OF UPWELLING

Robert Thomas Pearson

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THESIS

A COMPUTER SIMULATION MODEL
OF SEASONAL VARIATIONS IN OCEAN PRODUCTION
FOR A REGION OF UPWELLING

by

Robert Thomas Pearson

Thesis Advisor: Eugene D. Traganza

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A Computer Simulation Model of Seasonal Variations in Ocean Production for a Region of Upwelling

by

Robert Thomas Pearson
Lieutenant, United States Navy
B.S., Oregon State University, 1970

Submitted in partial fulfillment of the
requirements for the degree of

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I. INTRODUCTION

A. PURPOSE

There presently exists a large body of detailed information about the biological, physical, and chemical processes which occur in the marine environment. These processes act in concert to control the plankton populations of the sea. The analysis and interpretation of these environmental and biological factors has been significantly enhanced by the development of computer simulation techniques. The aim of computer modeling is to reproduce the dynamic response of a biological ecosystem to the complex mix of interacting variables which act on and within that system.

The purpose of this research was threefold:

(1) to formulate a model of a planktonic ecosystem in a region of upwelling,

(2) to develop a computer simulation of the model which generates seasonal changes in mixed layer nutrient concentrations, phytoplankton biomass carbon, and zooplankton biomass carbon, and

(3) to test the accuracy of the simulation results by comparison with observed data.

B. CONCEPTUAL MODEL

The first step in the modeling process consists of reducing the natural system being simulated to a simplified conceptual model. From this conceptual model, processes and rates are formulated into mathematical equations. The model is completed by translating the equations into the proper

format. The conceptual model considered here describes the relationships between factors controlling biological productivity (see Fig. 1).

1. Production

The synthesis of organic compounds from the inorganic constituents of the sea by the activity of living organisms is termed "production" (Tait and DeSanto, 1972). This synthesis is carried out almost exclusively by the photosynthetic activity of marine plants. The raw materials for photosynthesis are water, carbon dioxide and various nutrients, mainly inorganic ions of nitrogen (NO_3^-, NO_2^-, NH_3^+) and phosphorus ($PO_4^{\equiv}$, $HPO_4^{=}$, $H_2PO_4^-$). The chlorophyll-containing plants utilize light energy ($nh\gamma$) to synthesize higher energy organic compounds from the lower energy inorganics as follows:

$$6nh\gamma + 6CO_2 + 6H_2O \rightarrow 6CH_2O + 6O_2 \qquad (1)$$

This synthesis is referred to as "gross primary production."

A certain percentage of this synthesized material is broken down by the plant cells to provide energy to carry on physiological processes. This loss is termed respiration. The remainder of the synthesized material is available for cell growth and replication and is referred to as "net primary production." It is the net primary production of phytoplankton that is available for consumption by the herbivorous zooplankton.

Grazing by herbivores on the phytoplankton leads to "secondary production." Herbivores in turn are a food source

for first level carnivores ("tertiary production"), who themselves become prey for other carnivores, and so on. This type of organization of a biological community is referred to as a "trophic structure" or "food chain." At each level losses of biomass may occur from respiration, excretion, predation, or natural mortality. In reality the relationships are more complicated than this simple "food chain" concept indicates. Since one organism may take food from more than one trophic level, a more correct structure would define an intricate "food web."

In spite of its over-simplification, the "food chain" model depicts certain important characteristics of the marine planktonic ecosystem. First, the path of energy in the form of organic material is part of a closed cycle in which nutrients are assimilated, transferred, and regenerated; and, since water and carbon dioxide are abundant in the sea, the factors which potentially limit photosynthesis are the availability of nutrients and light energy to the phytoplankton (Ryther, 1963), and the temperature of the medium (Parsons and Takahashi, 1973).

2. Light

The light energy available to the phytoplankton is dependent on two parameters, the amount of radiation incident on the sea surface (usually expressed as g-cal/cm^2/min) and the transparency of the water (expressed as the extinction coefficient, k). Ryther (1956) observed that photosynthesis increases linearly with light intensity up to a saturation

point. Beyond this level greater illumination produces no further increase in photosynthesis and eventually results in an inhibition of the photosynthetic rate.

Light penetrating into the water is absorbed and scattered selectively. The intensity is attenuated exponentially with depth and can be expressed in terms of the extinction coefficient (k):

$$I_z = I_o e^{-kz} \tag{2}$$

I_o = radient energy at the surface

I_z = radient energy at depth z

k = light extinction per meter depth.

The transparency of the water is dependent on the concentration of phytoplankton and the presence of particulate or dissolved substances which absorb light. If we disregard selective absorption of light of different wavelengths and consider the total visible spectrum, we may say that for clear ocean water, k equals 0.04 - 0.05 (Ryther, 1963). Riley (1956) determined empirically the relationship between phytoplankton density and transparency. He assumed that absorption by material other than water and plants was negligible. His relationship is:

$$k = 0.04 + 0.0088\ C1 + 0.054\ C1^{2/3} \tag{3}$$

where C1 is chlorophyll concentration (μg/1) and 0.04 is the extinction coefficient for pure sea water. It is apparent from this formula that one mechanism for limiting phtoplankton

productivity is self-shading. Higher concentrations of algae produce a higher extinction coefficient and, from equation (2) reduce the light intensity in the water column. The reduced intensity lowers the rate of photosynthesis.

Measurements of the photosynthetic rate under conditions of bright daylight indicate that radiation intensity near the surface is at or above the saturation point for most phytoplankton. Under these conditions maximum productivity occurs at a depth, usually between 5 - 20 m. Below the depth of maximum productivity the photosynthetic rate decreases as the light intensity is attenuated. A point is reached where the rate of photosynthesis is just sufficient to balance the rate of breakdown of organic materials by respiration. This point is referred to as the "compensation depth" (Tait and DeSanto, 1972).

A second level below the compensation depth is the "critical depth." The concept of the "critical depth" was first suggested by Grann and Braarud (1935) and developed into a mathematical model by Sverdrup (1953). The critical depth is the level at which the total respiration of the phytoplankton in the water column just equals the total photosynthesis. The distance between the compensation depth and the critical depth depends on the proportion of the phytoplankton stock above and below the compensation depth.

If the standing stock of phytoplankton is to increase, its total phtosynthesis must be greater than its total respiration. This is possible as long as the depth to which

the plankton is mixed does not exceed the critical depth. When the depth of the mixed layer extends below the critical depth (assuming uniform plankton mixing), total losses exceed total gains and the stock declines.

3. Nutrients

Another parameter which can critically limit the growth of phytoplankton is the concentration of inorganic nutrients in the upper, "euphotic" layers of the ocean. Many elements such as manganese, silicon, copper, molybdenum, and cobalt are essential for the growth of particular species. However, ions of nitrogen and phosphorous may be present in sufficiently low concentrations that their availability exerts a dominant control over production (Tait and DeSanto, 1972).

The absorption of nutrients in the surface layer by phytoplankton can reduce the concentration of these ions to levels where further uptake is inhibited. The kinetics of this inhibition was investigated by Ketchum (1939). He demonstrated that the uptake of nitrate by the diatom *Nitzschia closterium* was concentration dependent over the approximate range of 1 - 7 μg-atom N/1. He also showed that phosphate followed a similar inhibition. Dugdale (1967) described the rate of nutrient uptaking using Michaelis-Menten enzyme kinetics in which:

$$v = V_{max} \frac{N}{K_s + N} \tag{4}$$

v = rate of nutrient uptake

V_{max} = maximum rate of nutrient uptake

K_s = half saturation constant, i.e. the nutrient concentration at which $v = V_{max}/2$.

N = nutrient concentration

Studies conducted by Eppley and Thomas (1969) on two species of diatoms indicate that the half-saturation constants for growth and nutrient uptake are very similar. This means that the expression given for velocity of nutrient uptake can also be used to describe the growth rate;

$$\mu = \text{max}\ \frac{N}{K_s + N} \tag{5}$$

μ = growth rate

μ_{max} = maximum growth rate

By plotting N/μ versus N, a straight line is obtained with the intercept on the abscissa at $-K_s$.

a. Temperature

Ichimura (cited in Parsons and Takahashi, 1973) studied the relationships between phosphate concentration and the rates of organic synthesis in natural populations of phytoplankton in Tokyo Bay. His results indicate a definite Michaelis-Menten type response which is highly temperature dependent (see Fig. 2).

b. Excretion

A certain fraction of the nutrients absorbed by phytoplankton are returned to the medium both in the euphotic zone and at depth by zooplankton. According to Harvey (1957), nearly all phytoplankton is grazed by herbivorous zooplankton. A portion of this grazed algae can be voided in an undigested or semidigested state. It is unclear, however, how much phytoplankton nutrient elimination by zooplankton is returned

in an available form in the euphotic zone and how much sinks to greater depths before being remineralized. Some authors (Gardner, 1937; Riley, 1951; and Harris, 1959) consider zooplankton to be a significant source of useable nutrient in the euphotic zone, while others believe this source to be negligible (Steele, 1959; Rigler, 1971). Most recent work seems to favor the higher estimates. A distribution of dietary phosphorus in Calanus during active feeding (April) has been given by Butler et al. (1970) as 17.2% retained for growth, 23.0% voided as fecal pellets and 59.8% excreted as soluble phosphorus (organic and inorganic). These estimates indicate that over 80% of the phosphorus ingested by Calanus gets back into the environment and nearly 60% is soluble phosphorus. The ability of marine algae to utilize soluble organic phosphorus was demonstrated by Kuenzler (1965).

The importance of zooplankton as a source of phytoplankton nutrients was verified in two studies cited by Parsons and Takahashi (1973). Cushing (P. 139) "showed that during ten weeks of the spring phytoplankton/zooplankton bloom in the North Sea, inorganic phosphate did not decrease below 0.6 μg-atom/l due to zooplankton excretion. However, Antia et al. (1963) observed a decrease in phosphate to 0.1 μg-atom/l after two weeks of phytoplankton growth in the absence of zooplankton," suggesting the important role of zooplankton as a source of phytoplankton nutrients.

The nitrogen and phosphorous cycles in the sea follow basically the same course. However, the remineralization

of nitrogen occurs at a much slower rate than phosphorus. In the experiment conducted by Antia et al. (1963) half the phytoplankton phosphorus was remineralized in 14 days, but after 75 days no remineralization of nitrogen was observed.

A second major difference between the cycles is that all three inorganic nitrogen compounds, ammonium (NH_4^+), nitrite (NO_2^-), and nitrate (NO_3^-) can be absorbed by phytoplankton. Absorption is not indiscriminate, however. There is a marked preferential uptake of ammonium (Dugdale and Goering, 1967). The nitrogen cycle then consists of three seperate cycles, one for each of the three nitrogen containing ions involved in photosynthesis, and possibly a fourth involving urea (Dugdale, personal communication).

Although a fraction of the nutrients absorbed by the phytoplankton during photosynthesis are recycled within the euphotic zone, the remainder are regenerated in deeper water. The result is a net depletion of nutrients from surface waters and an accumulation of nutrients at depth. The continuation of plant growth in the sea, therefore, is largely dependent upon the various processes which return nutrient-rich water from below the euphotic zone.

c. Mixing and Upwelling

Turbulent (eddy) diffusion is a primary mechanism of injecting nutrients into surface waters of many ocean areas. Vertic~~le~~al eddies may be generated by a variety of dynamic forces including thermal convection, internal waves, friction at current boundaries, and wind-mixing. Turbulence may have

a variety of effects on biological production. It may enhance production by bringing nutrients to the surface, or it may reduce production by carrying phytoplankton down below the euphotic zone.

A second major phenomenon operating in more localized regions is coastal upwelling. For example, along western continental boundaries in the Northern Hemisphere a northerly wind stress blowing parallel to the coast causes an offshore transport of water with a compensating replacement of upwelled waters from 200-300 m depth (Sverdrup et al., 1942).

An index of the intensity of upwelling has been estimated using wind stress data (Wooster and Reid, 1963; Bakun, 1973). This "Ekman transport" of water away from the coast is calculated according to the following equation:

$$M_n = \tau_p/f \qquad (6)$$

M_n = "Ekman transport" normal to the coast
τ_p = Wind stress parallel to the coast
f = Coriolis parameter

Using the magnitude of offshore transport it is possible to compute the velocity of the associated verticle motion. Wooster and Reid (1963) assumed a steady-state offshore "Ekman transport" of 10 kg/cm/sec with a coastal upwelling band 50 km wide and estimated the compensating vertical motion to be about 50 m/month, a resut compatible with previous estimates which ranged from 10-20 m/month to

80 m/month (Smith, 1968). Although the depth from which these waters are upwelled is not believed to exceed a few hundred meters, the input of nutrients is sufficient to maintain the regions of upwelling at a high level of productivity.

Horizontal advection of surface waters could have either a positive or negative effect on nutrient concentration. If "upstream" or "offshore" waters have been depleted below local values, advection into the area under consideration would reduce the concentration and conversely, higher values would raise local concentrations. This process is discussed later.

4. Grazing

Another major factor controlling the productivity of phytoplankton is grazing by herbivorous zooplankton. According to a number of authors (Steemann-Nielsen, 1958; Cushing, 1959; Steele, 1974) grazing by zooplankton is the primary factor affecting the dynamics of plankton populations.

Mullin (1963) identified two methods of describing zooplankton grazing activity, by the "filtering rate" and the "food intake rate." The "filtering rate" is the rate at which water is swept clear of food organisms. The "rate of food intake" is a measure of the biomass of food organisms ingested per unit time and depends on the filtering rate and the concentration and size of the food organisms. Mullin (1963) demonstrated that, for four species of copepods, the volume swept clear is inversely proportional to food concentration. Steele (1974) showed that such an inverse relation

corresponds to a hyperbolic rate of intake of biomass. As the food concentration increases, the rate of biomass ingestion approaches a maximum (see Fig. 3). McAllister (1970) observed intake rates which approximate the type given by Steele. Wash and Bass (1971) expressed this saturation feeding behavior in terms of a Michaelis-Menten equation. This hyperbolic response suggests two important characteristics of herbivore grazing. First, a minimum phytoplankton concentration exists at which grazing ceases; and second, as algal concentration increases, herbivores asymptotically approach a maximum ingestion rate.

In summary, it is apparent that the productivity of a region is dependent on the availability of light and nutrients to the phytoplankton, the temperature of the medium, and the grazing and excretion of biomass and nutrients by the herbivores. The rates at which these processes proceed are not simple functions but are dependent on a complex mix of physical, chemical, and biological parameters. In order to model the dynamics of this regional plankton community, therefore, it is essential to utilize a method of computer simulation. Simulation provides a technique for integrating the many variables affecting productivity into a system of interacting components.

II. BACKGROUND THEORY

A. EARLY WORK

The basic equations of biological growth kinetics were developed in the early 1920's by A. J. Lotka (1925). Volterra (1926) extended Lotka's equations to describe predator-prey interactions. The Lotka-Volterra equations (7) consist of a pair of differential equations in which the growth of each population is limited by two factors, self inhibition (r_1, r_2) and competition (a, b) (Odum, 1971):

$$\frac{dN_1}{dt} = r_1 N_1 \frac{K_1 - N_1 - aN_2}{K_1} \tag{7}$$

$$\frac{dN_2}{dt} = r_2 N_2 \frac{K_2 - N_2 - bN_1}{K_2}$$

N_1, N_2 = quantity of species one and two

a, b = competition coefficient indicating the negative effect one species has on the other

r_1, r_2 = the intrinsic growth rates of each species

K_1, K_2 = carrying capacity, the largest population of each species the environment can support.

Fleming (1939) used a modified form of the Lotka-Volterra equations to calculate the seasonal change in phytoplankton population:

$$\frac{dP}{dt} = P(a - (b + ct)). \tag{8}$$

P = Integral phytoplankton population under a unit of water surface

a = specific growth rate of plankton

b = initial grazing rate

$(b+ct)$ = grazing rate as a function of time

c = rate of grazing rate change

t = time.

His model emphasizes grazing as the factor limiting phytoplankton populations. Patten (1968) pointed out that, although the model may be unrealistic in specifying a constant growth rate and a linearly increasing grazing rate, the model "worked" because it accurately corresponded to observations made by Harvey et al. (1935) in the English Channel.

B. PHYTOPLANKTON MODEL

Riley (1946) made a significant improvement upon the lack of realism in Fleming's model. He defined the change in phytoplankton as:

$$\frac{dP}{dt} = P(P_h - R - G) \qquad (9)$$

P = integral phytoplankton under a square unit of water surface.

P_h = photosynthetic rate

R = respiration rate

G = grazing rate.

Instead of using a constant photosynthetic rate, Riley defined P_h as a function of light intensity, nutrient concentration and verticle turbulence.

$$P_h = (pI_o/kz_1)(1 - e^{-kz_1})(1 - N)(1 - V) \qquad (10)$$

P = fraction of light used in photosynthesis

I_o = surface light intensity

k = extinction coefficient

z_1 = depth of euphotic zone

N = nutrient depletion factor

V = factor expressing the effect of turbulence

His expression for the respiration rate was defined in terms of temperature:

$$R = R_o e^{rT} \qquad (11)$$

R = respiration rate

R_o = respiration rate at 0°C

r = rate of respiration rate change

T = temperature.

The grazing rate was assumed to be proportional to the integral quantity of zooplankton;

$$G = gZ \qquad (12)$$

G = grazing rate

g = proportionality constant between grazing rate and zooplankton

Z = integral zooplankton under a square unit of water surface.

C. PHYTOPLANKTON, NUTRIENT MODEL

Steele (1958) introduced a model based largely on the equations developed by Riley. His contribution is significant in that it is one of the first "systems" approaches to plankton

dynamics. Where Riley treated nutrient concentration as an independent parameter, Steele defined nutrients and phytoplankton as two inter-dependent variables.

To develop a nutrient equation, Steele made certain simplifying assumptions about the environment. The ocean volume was divided into two thermally-stratified layers with homogeneous mixing in each layer. Mixing across the boundary was controlled by an exchange coefficient (m).

The system of equations devised by Steele define the rate of change of nutrients and phytoplankton in a surface layer 40m deep:

$$\frac{dP}{dt} = (p_h - r - fz)P - \frac{vP}{40} - m(P - P_o) \qquad (13)$$

$$\frac{dp}{dt} = -c(p_h - r)P - m(p - p_o) \qquad (14)$$

m = mixing coefficient governing exchange between the upper and lower layers.

P = phytoplankton concentration in the upper layer.

P_o = phytoplankton concentration in the lower layer.

p_h = photosynthetic rate

r = phytoplankton respiration rate

f = grazing rate, a function of zooplankton populations

z = zooplankton population

v = ratio of sea water viscosity at 0°C to that at ambient temperature

c = factor for converting carbon to phosphate

p = nutrient concentration in upper layer

p_o = nutrient concentration in lower layer.

D. REGIONAL STEADY STATE MODEL

Riley (1965) added to Steele's (1958) model a term expressing the regeneration of nutrients voided by zooplankton. This model was tested against observations made during quasi-steady state summer conditions found in various regions of the Atlantic and Pacific Oceans. Basic environmental variables, including phosphate concentration in the deep water mass, the rate of mixing between the two layers, and water temperature, were varied according to the characteristics of each area. For each array of environmental factors, steady-state concentrations of phytoplankton, zooplankton, and phosphate were calculated for the upper layer. Riley concluded that the model "provided a reasonable fit for most of the observed variations."

E. SHORT TERM SPATIAL MODEL

Walsh and Bass (1971) developed a spatial model of an upwelling ecosystem which was used for short term analysis. Their system of equations related the upwelling of nutrients to the nitrogen biomass of phytoplankton, zooplankton, and fish. A Michaelis-Menten type expression was incorporated into the model to define both the nutrient uptake rate and the grazing rate.

To conclude, the early models of Riley (1946) and Steele (1958) established the fundamental principles used in simulating plankton dynamics. Riley (1965) demonstrated that regional variations in phytoplankton could be

realistically predicted for a quasi-steady state summer period. Using local environmental conditions as input parameters, his model accurately predicted the plankton stocks observed in different geographic areas. Walsh and Bass (1971) developed a spatial model to analyze a specific region of upwelling. Since their model applied to short term (two week) simulations, environmental parameters were held constant.

III. THE MODEL

The simulation model proposed in this thesis defines a one dimensional, nonlinear, planktonic ecosystem in a centralized region of coastal upwelling (Monterey Bay). The simulation output consists of a theoretical annual cycle of mixed layer nutrient concentration, phytoplankton and zooplankton biomass. Although the model has been developed for a localized area it may be considered applicable to a broader geographic region. Bolin and Abbott (1962) determined that "results obtained (for the Monterey Bay area) should reflect in a broad way the oceanographic conditions and events occurring over an extensive segment of the eastern North Pacific." As in Riley's (1965) model, environmental conditions control the output of the system. From observed changes in the physical environment, the model generates values for phosphate concentration and plankton standing stocks.

A. COMPARTMENT MODEL

The compartment model (Fig. 1) defines the flow of nutrients and organic carbon through a three component ecosystem consisting of inorganic phosphate, phytoplankton, and herbivorous zooplankton. In this diagram (method from Patten, (1971)) the state variables of the system are denoted by blocks, and signal flows between the "compartments" are

designated by unidirectional branches. The relations between the state variables are expressed as a system of differential equations.

The three equations in Fig. (1) describe the change in phosphate concentration in the mixed layer (X1), in the biomass of phytoplankton (X2), and in the biomass of herbivorous zooplankton (X3). The underlying principle used in the derivation of these expressions is the conservation of mass. Therefore, the validity of the system of equations depends on having all significant transfers of matter accounted for.

The movement of substance or energy into or through the system is termed a "flux" or "flow" and is described as a quantity of mass or energy per unit time, e.g., gram calories per square centimeter per day or grams carbon per square meter per day. In ecological systems the flux between compartments is often dependent upon the state variables involved. In such cases the flux is defined in terms of a "rate of transfer" or "flow rate." A flow rate is a quantity transferred per unit quantity of source or receiver, per unit time. The distinction between flux and flow rate can best be made in terms of units. If a flux is in grams carbon per square meter per day, the corresponding rate of flow is in units of reciprocal days.

To differentiate between fluxes and flow rates in the model, fluxes have been denoted by descriptive variable names (NUT, REGEN, GRAZ, etc.). Flow rates are designated by a Greek letter followed by two digits (TAU12, RHO30, LAM30, etc.).

"TAU" identifies a transfer between tropic levels, "RHO" signifies respiration, and "LAM" represents losses due to mortality and carnivorous predation. The first digit following the Greek letter identifies the source compartment and the second, the receiver. A zero indicates a flow into or out of the system.

B. ECOSYSTEM INPUTS AND BOUNDARY CONDITIONS

Inputs which originate as energy or material sources outside the system act as forcing functions. The forcing functions which drive the system of equations consist of four environmental parameters, incident solar radiation (RADI), sea surface temperature (TEMP), a coefficient of water volume exchange across the layer (M), and an estimate of upwelling velocity (W).

Values for incident solar radiation (RADI) were obtained from tables developed by Kimball (p. 103, in Sverdrup et. al., 1942). The values desired for latitude 36° N. were estimated by interpolating between those tabulated for 42° N. and 30° N.

Temperature data was obtained during a series of seven cruises conducted aboard the R/V ACANIA from February through November 1974. Estimates of the mixed layer depth (Z), used to define boundary conditions, were developed from the empirical formula of Robinson and Bauer (1971). This formula, currently used by Fleet Numerical Weather Central (FNWC) defines the mixed layer depth as "The depth at which the temperature of the water is 2° F. (1.11° C) below the surface temperature."

Bakun (1973) developed a series of monthly indices describing the intensity of large scale, wind induced coastal upwelling at selected locations along the west coast of North America. The indices are based on calculations of offshore Ekman transport derived from monthly mean surface atmospheric pressure data. Values of offshore transport for 1974 (Bakun, Personal Communication) were used to estimate upwelling velocity (W). A maximum velocity of one meter per day was assumed to correspond with the maximum index of upwelling. A linear interpolation was then applied to other monthly indices to arrive at an annual variation of upwelling velocity. The coefficient of exchange (M) was assigned a constant value of 0.12. Other sources of nutrient input (i.e., river runoff etc.) have been assumed to be negligible.

As mentioned earlier, the models of Steele (1958) and Riley (1965) postulated a two layered ocean with homogeneous mixing in each layer. Phytoplankton growth was confined to the upper layer and the phosphate concentration was assumed to remain constant in the lower layer. Mixing between the two layers supplied nutrients to the surface. The present model incorporates these assumptions and includes upwelling as an additional source of nutrient input.

C. ECOSYSTEM EQUATIONS

Having specified the input signals and boundary conditions, it is possible to define a system of equations to generate the response of the state variables to variations observed in the physical environment.

1. Nutrient Equation

The first equation, expressing the change in phosphate concentration in the mixed layer, is given by:

$$\frac{dX1}{dt} = NUT + REGEN - UPTAK \qquad (15)$$

i.e.:

The change in nutrient concentration with time	(=)	The input of nutrient from upwelling and mixing	(+)	The regeneration input from zooplankton excretion	(-)	The loss due to photosynthetic uptake by phytoplankton.

The expression defining the input of nutrients from the lower layer is:

$$NUT + ((W/EKL)*(DX1-X1)) + ((M/Z)*(DX1-X1)) \qquad (16)$$

NUT = flux of nutrients into the surface layer (μg atom P/1/day)

W = upwelling velocity (m/day)

EKL = depth of Ekman layer (m)

DX1 = nutrient concentration in the deep layer (μg atom P/1)

X1 = nutrient concentration in the mixed layer (μg atom P/1)

M = coefficient of exchange (m/day)

Z = mixed layer depth (m).

The ratio of the coefficient of exchange to the mixed layer depth (M/Z) represents the fraction of the upper layer transferred to the lower layer in a days time, with a corresponding replacement from below. The ratio of the upwelling velocity to the depth of the Ekman layer (W/EKL)

represents the fraction of the surface water that is transported offshore and replaced by upwelled water.

The second term in the nutrient equation represents the input of phosphate from the nutrients voided by zooplankton:

$$\text{REGEN} = \text{TAU31} * \text{X3} \tag{17}$$

REGEN = flux of nutrients from zooplankton (μg-atom/l/day)

TAU31 = rate of input of phosphate into the nutrient pool by zooplankton (μg-atom/l/g C/m^2/day)

X3 = standing stock of zooplankton (g C/m^2).

The rate at which nutrients, voided by zooplankton, are made available for phytoplankton uptake is a function of the grazing rate of the zooplankton.

$$\text{TAU31} = \text{FAVL} * (C/Z) * \text{TAU30} \tag{18}$$

TAU31 = rate of input of phosphate to the nutrient pool by zooplankton (μg-atom/l/g C/m^2/day)

FAVL = fraction of voided nutrient made available for phytoplankton uptake (dimensionless)

C = converts biomass to nutrients voided. (μg-atom/l/g C/m^3)

Z = depth of the mixed layer (m)

TAU30 = rate at which biomass is voided by zooplankton (day^{-1}).

The rate at which biomass is voided is dependent upon the grazing rate (see equation 37).

The final term in the nutrient equation is an expression for the loss of phosphate to phytoplankton:

$$UPTAK = C * TAU12 * (X2/Z) \tag{19}$$

UPTAK	= flux of nutrients to phytoplankton	(μg atom P/1/day)
C	= a conversion factor relating organic carbon to phosphate	(μg atom P/1/g C/m^3)
TAU12	= rate of organic production by a unit of phytoplankton	(day^{-1})
X2	= standing stock of phytoplankton	(g C/m^2)
Z	= mixed layer depth	(m).

2. Phytoplankton Equation

The equation for the second state variable, phytoplankton, is an adaptation of Riley's (1946) model. Modifications have been made on the basis of recent findings, e.g., the effects of a potentially limiting nutrient on photosynthesis have been expressed in terms of Michaelis-Menten kinetics (Dugdale 1967); McAllister (1970) demonstrated that zooplankton grazing could be defined in terms of saturation feeding; and, Walsh and Bass (1971) used a form of the Michaelis-Menten expression to describe both the effects of nutrient limitation in photosynthesis and the saturation response in zooplankton grazing. The approach of Walsh and Bass has been followed here.

The differential equation for the change in phytoplankton biomass carbon is:

$$\frac{dX2}{dt} = PROD - RESP2 - GRAZ \tag{20}$$

which in word form is:

The change in phytoplankton biomass with time	(=)	The production by photosynthesis	(−)	The loss due to respiration	(−)	The loss to grazing by zooplankton.

The expression defining primary production is a product of the photosynthetic rate and the phytoplankton biomass:

$$PROD = TAU12 * X2 \tag{21}$$

PROD = photosynthetic flux to phytoplankton biomass (g C/m^2/day)

TAU12 = rate of organic production by a unit of phytoplankton (day^{-1})

X2 = standing stock of phytoplankton (g C/m^2).

Since photosynthesis in the ocean may be limited by temperature, light, or nutrients, each of these parameters must appear in the rate equation:

$$TAU12 = P * RAD * NTLIM \tag{22}$$

TAU12 = rate of organic production by a unit of phytoplankton (day^{-1})

P = photosynthetic constant, converts light energy units to photosynthetic potential (g cal/cm^2/min)$^{-1}$

RAD = mean radiant energy available in a water column of depth (Z) (g cal/cm^2/min)

NTLIM = potential photosynthetic rate, a function of temperature and phosphate concentration (day^{-1}).

The value for the radiant intensity at depth Z (RADZ) is derived from the incident intensity (RADI) as follows:

$$RADZ = RADI * \exp(-K*Z) \tag{23}$$

RADZ = intensity at depth Z (g cal/cm^2/min)

RADI = incident intensity (g cal/cm^2/min)

K = extinction coefficient (m^{-1})

Z = mixed layer depth (m)

To find the mean radiant energy (RAD) between the surface and the mixed layer depth (Z), equation eight is integrated from zero to Z and devided by Z,

$$RAD = (RADI/Z) * \int_0^Z \exp(-K*Z)dZ$$

$$RAD = (RADI/(-K*Z)) * (1.0 - \exp(-K*Z)) \tag{24}$$

where $\exp(-K*Z) = 1.0$ at the surface.

The extinction coefficient (K) was estimated using Riley's (1956) empirical formula;

$$K = 0.04 + (0.0088 * CL) + (0.054 * CL)\ 2/3 \tag{25}$$

K = extinction coefficient (m^{-1})

CL = chlorophyll concentration (mg/m^3).

Riley (1959) indicated that carbon:chlorophyll ratios may vary from 30 to 128. During periods of algal growth, the ratio approaches the lower limit. It has been assumed that phytoplankton densities are significant during this rapid growth phase. Therefore, the lower ratio of 30 was used. Using this ratio, the value for the chlorophyll concentration becomes:

$$CL = 33.33 * (X2/Z).$$

The function NTLIM (Fig. 2) defines the maximum photosynthetic rate possible for a given combination of temperature and phosphate concentration. The function approximates the results of Ichimura (p. 72, in Parson and Takahashi, 1971):

$$NTLIM = MAXN * (X1 - X1MIN)/(KN + (X1 - X1MIN)) \quad (27)$$

NTLIM = photosynthetic rate as a function of nutrient concentration and temperature (day^{-1})

X1 = nutrient concentration in the mixed layer (μg atom/l)

X1MIN = minimum nutrient concentration below which phytosynthesis will not occur (μg atom/l)

KN = half saturation constant (μg atom/l).

The value for MAXN is defined as a function of temperature:

$$MAXN = S * TEMP + B \quad (28)$$

MAXN = maximum rate of photosynthesis at a given temperature (day^{-1})

S = rate of change of MAXN with temperature ($day^{-1}/°$)

B = MAXN at 0°C (°C)

TEMP = mixed layer temperature (°C).

In summary, the actual photosynthetic rate for a specified set of light conditions, nutrient concentration, and temperature is a product of the photosynthetic potential (P*RAD) and the maximum possible rate (NTLIM). The second term in the phytoplankton equation represents the loss of

biomass from respiration:

$$RESP2 = RHO20 * X2 \qquad (29)$$

RESP2 =	flux of biomass expended by cell respiration	(g C/m^2/day)
RHO20 =	rate of respiration per unit of phytoplankton	(day^{-1})
X2 =	standing stock of phytoplankton	(g C/m^2).

Phytoplankton respiration rate is defined as a function of temperature following Riley (1946):

$$RHO20 = RHOZ2 * \exp(R*TEMP) \qquad (30)$$

RHO20 =	rate of respiration per unit of phytoplankton	(day^{-1})
RHOZ2 =	rate of respiration at 0°C.	(day^{-1})
R =	constant, rate of change in respiration rate with temperature	($°C^{-1}$)
TEMP =	mixed layer temperature	(°C).

The final expression in the phytoplankton equation represents the loss of biomass to grazing by herbivorous zooplankton:

$$GRAZ = TAU23 * X3 \qquad (31)$$

GRAZ =	flux of biomass from phytoplankton to zooplankton	(g C/m^2/day)
TAU23=	zooplankton grazing rate	(day^{-1})
X3 =	standing stock of zooplankton	(g C/m^2).

A saturation grazing rate is defined by a Michaelis-Menten type equation (Fig. 3) following Walsh and Bass (1971):

$$\mathrm{TAU23} = \mathrm{MAXG}*(\mathrm{X2MG}-\mathrm{X2MIN})/(\mathrm{KG}+(\mathrm{X2MG}-\mathrm{X2MIN})) \tag{32}$$

TAU23 = zooplankton grazing rate (day^{-1})

MAXG = maximum specific grazing rate (day^{-1})

X2MG = concentration of phytoplankton in a mixed layer (mg C/m^3)

X2MIN = minimum concentration of phytoplankton below which grazing will not occur (mg C/m^3)

KG = half saturation constant (mg C/m^3).

3. Zooplankton Equation

The zooplankton equation is:

$$\frac{dX3}{dt} = \mathrm{GRAZ} - \mathrm{RESP3} - \mathrm{VOID} - \mathrm{LOSS}$$

which in words is:

The change in zooplankton biomass with time (=) The input from grazing on phytoplankton biomass (−) The loss of biomass from respiration (−) The loss of biomass by excretion

(−) The loss of biomass by predation and mortality

The first term (GRAZ) in this equation has been defined (see eq. 31). The second term is a temperature dependent respiration term similar to that for phytoplankton:

$$\mathrm{RESP3} = \mathrm{RHO30} * \mathrm{X3} \tag{34}$$

RESP3 = flux of biomass during respiration (g C/m^2/day)

RHO30 = rate of respiration per unit of zooplankton (day^{-1})

X3 = standing stock of zooplankton (g C/m^2).

The equation for the respiration rate is:

$$\mathrm{RHO30} = \mathrm{RHOZ3} * \exp(\mathrm{R}*\mathrm{TEMP}) \tag{35}$$

RHO30 = rate of respiration per unit of zooplankton (day^{-1})

RHOZ3 = rate of respiration at 0°C. (day^{-1})

R = rate of change in respiration rate as a function of temperature ($°\mathrm{C}^{-1}$)

TEMP = mixed layer temperature (°C).

The loss of biomass by excretion is:

$$\mathrm{VOID} = \mathrm{TAU30} * \mathrm{X3} \tag{36}$$

VOID = flux of voided biomass ($\mathrm{g\ C/m^2/day}$)

TAU30 = rate of excretion per unit of zooplankton biomass (day^{-1})

X3 = standing stock of zooplankton ($\mathrm{g\ C/m^2}$).

Based on data collected by Harvey et. al. (1935) and his own observations, Riley (1947) concluded that utilization (ratio of assimilation to ingestion) of grazed phytoplankton was very nearly unity when algal concentrations were low. During such periods, therefore, minimal carbon biomass would be voided. However, with the onset of the spring flowering, more food was available than could be used, so that quantities were voided in a semidigested condition. To approximate these observations, the fraction of biomass voided has been treated as a function of the grazing rate:

$$\mathrm{TAU30} = (0.8*(\mathrm{TAU23}/\mathrm{MAXG})) * \mathrm{TAU23} \tag{37}$$

TAU30 = rate of excretion per unit of zooplankton biomass (day^{-1})

TAU23 = zooplankton grazing rate (day^{-1})

MAXG = maximum specific grazing rate (day^{-1}).

When grazing rates are low (.025 day^{-1}), the bulk of the ingested phytoplankton is assimilated (92%) and only 8% is voided. During the bloom conditions observed in March 70% of the grazed biomass was assimilated with 30% being voided. These values are in general agreement with Conover's (p. 113, in Parsons and Takahashi, 1973) conclusion that, in general, zooplankton assimilation efficiencies range from 60 to 95%.

The final term in the zooplankton equation represents losses of zooplankton biomass by predation and natural mortality.

$$\text{LOSS} = \text{LAM30} * \text{X3} \tag{38}$$

LOSS = flux of biomass due to predation and mortality ($\text{g C/m}^2\text{/day}$)

LAM30 = rate of loss per unit of zooplankton (day^{-1})

X3 = standing stock of zooplankton (g C/m^2).

The rate of loss has been estimated by this author as a constant 1% of the standing stock per day.

$$\text{LAM30} = \text{L} \tag{39}$$

L = fraction of zooplankton lost per day (day^{-1}).

TABLE I

VALUES FOR EQUATION CONSTANTS AND THEIR RESPECTIVE SOURCES

NAME	DEFINITION	VALUE	REFERENCE
B	MAXN at 0°C	0.50	estimate
C	phosphate:carbon ratio	0.774	Riley (1965)
DX1	nutrient concentration	3.0	estimated from data
EKL	depth of Ekman layer	50.0	Smith (1968)
FAVL	nutrient regeneration coefficient	0.8	Butler, et al., (1970)
KG	half saturation constant for zooplankton grazing	80.0	McAllister (1970)
KN	half saturation constant for phytoplankton grazing	0.6	Ichimura, (in Parsons and Takahashi, 1973)
L	zooplankton loss rate	0.01	estimate
M	coefficient of exchange	0.12	estimate
MAXG	maximum grazing rate	0.25	McAllister (1970)
P	photosynthetic constant	2.5	Riley (1946)
R	respiration coefficient	0.069	Riley (1946)
RHOZ2	phytoplankton respiration at 0°C.	0.0175	Riley (1946)
RHOZ3	zooplankton respiration at 0°C.	0.019	Riley (1947)
S	rate of change of MAXN with temperature	0.13	estimate
X1MIN	minimum nutrient uptake concentration	0.0	Dugdale (1967)
X2MIN	minimum phytoplankton concentration for grazing	16.0	McAllister (1970)

IV. PROCEDURE

A. SIMULATION

The system of differential equations was integrated numerically using the System/360 Continuous Simulation Modeling Program (S/360 CSMP) available on the Naval Postgraduate School IBM-360 computer. A brief discussion of S/360 CSMP is given in the Appendix. A more complete description is available in the IBM User's Manual (1970).

B. DATA COLLECTION

Theoretical results, generated from observed environmental conditions (i.e., radiation, temperature, etc.), were compared with observed seasonal variations in phosphate concentration and zooplankton biomass carbon. Data was obtained on a series of cruises conducted aboard the R/V ACANIA from February through November, 1974. Dissolved reactive phosphate was measured using a Technicon II Auto-analyser. Concentrations in the mixed layer were determined by computing a "weighted mean" of measured values within the layer. The "weight" for each value was assigned according to the interval between sample depths.

Zooplankton samples were collected in a number three (333 μm mesh) net with a mouth diameter of c.a. 25 cm. The carbon content of each sample was determined using a high temperature dry combustion thermal conductivity method (Traganza, Radney, and Grahm, 1975). A complete listing

of cruise data including phosphate, temperature, and carbon values is available, (Traganza, 1975).

C. PARAMETER TESTING

The response of the model to different environmental conditions was examined by generating simulations using hypothetical values for environmental functions. The values of incident radiation (RADI), mixed layer temperature (TEMP), mixed layer depth (Z) and upwelling velocity (W) were varied 10% above and below their "standard value" (the observed or literature value). A seperate simulation was computed for each variation, leading to eight seperate cases. The variations tested are indicated in figure (4). The O's represent the standard or observed value, the +'s indicate a 10% increase, and the X's a 10% decrease.

V. RESULTS

A. COMPARISON OF SIMULATION WITH OBSERVED DATA

The initial simulation results are shown in Fig. (5). Theoretical cycles appear as asterisks and the observed cruise values are indicated by X's. The average difference between simulated and observed nutrient concentrations is 66.4%. A 94% average error exists between the simulated and observed standing stock of zooplankton. Although the absolute error is large, the trends of the data and simulation are quite similar. The principle source of error in the phosphate cycle was a 20 day variation between the simulated and observed nutrient minimum. The zooplankton simulation error was caused by the failure of the model to match the apparently low biomass values observed in late March and early September.

Seasonal changes in mean phosphate concentration in the mixed layer were characterized by a steady increase during winter and spring months from an initial value of 1.5 μg-atom/1 to a maximum 1.86 μg-atom/1. The simulated concentration was assigned an initial condition of 1.5 μg-atom/1 and subsequently increased to 1.99 μg-atom/1. In June a sharp decline in concentration occurred both in the data and in the simulation. A minimum value of 0.33 μg-atom/1 was observed in early August. The simulated minimum (0.61 μg-atom/1) occurred in late August. Both the theoretical and the measured

concentrations increased steadily from August through December culminating at 1.0 μg-atom/1.

The differences between observed and simulated maximum and minimum nutrient concentrations indicated that the function controlling nutrient uptake, NTLIM, (eq. 27) did not fit existing conditions. Testing various values of the constants KN, (eq. 27) S and B (eq. 28) indicated that a reduction in the value of KN from 0.6 μg-atom/1 to 0.3 μg-atom/1 produced a more accurate correspondence between measured and theoretical maximum and minimum phosphate concentrations (Fig. 6).

Phytoplankton data was not available for comparison with theoretical values. However, the sharp decline in nutrient concentrations during June and July suggests the presence of substantial phytoplankton stocks during this period. The simulated bloom, which peaks in July, correlates with the observed decline in phosphate. The phytoplankton maximum does not, however, precede the initial zooplankton peak as is normally observed.

The cycle of zooplankton biomass was characterized by two distinct maxima. The first peak (1.05 gC/m^2) was observed in late July. A simulated maximum (1.02 gC/m^2) occurred during the same period. This initial peak was followed by a sharp decline of measured biomass. A minimum of 0.18 gC/m^2 was observed in early September. A lesser reduction occurred in the theoretical values (0.78 gC/m^2). A rapid increase in the standing stock followed the September

minimum. An overall maximum of 1.85 gC/m^2 was observed in mid-December. Simulation values also increased producing a lesser maximum of 1.58 gC/m^2.

The simulated energetic balance observed in the zooplankton varied with changes in phytoplankton concentration and temperature. During the onset of the phytoplankton bloom in mid-March, zooplankton assimilated 70% of the ingested carbon biomass and voided 30%. Of that carbon which was assimilated 60% was lost through respiration. In mid-July, when phytoplankton stocks had peaked, the high algal concentration resulted in near maximum grazing rates. Because more biomass was being ingested than could be used, 77% was voided and 23% assimilated. Due to higher mixed layer temperatures, 75% of the 23% assimilated biomass was required for respiration.

Calculation of the annual average of monthly zooplankton gains and losses indicated 65% of the ingested phytoplankton biomass was assimilated, 35% was voided. Of the 65% assimilated biomass, 86% was respired leaving 14% (9% of that assimilated) for growth. Of this remaining biomass, 75% was lost to predation and natural mortality.

B. EFFECTS OF VARIATIONS IN ENVIRONMENTAL PARAMETERS

Additional simulations were generated to determine the response of state variables to changes in the environmental parameters. Table II lists the percent change each modified parameter produced in the phytoplankton and zooplankton

TABLE II

CHANGE IN MAXIMUM BIOMASS OBSERVED WITH ±10% CHANGE IN FORCING FUNCTIONS

	PHYTOPLANKTON	ZOOPLANKTON
RADI, -10%	-13%	-07%
RADI, +10%	+11%	+10%
LAYER, -10%	+01%	+02%
LAYER, +10%	-02%	-03%
UPWEL, -10%	-01%	-01%
UPWEL, +10%	00%	00%
TEMP, -10%	-10%	+85%
TEMP, +10%	+06%	-65%

standing stock maxima. Complete simulation results are given in Figures (7 - 10). The 10% increase in incident radiation produced a nearly equivalent gain in the maximum biomass of both phytoplankton and zooplankton (Fig. 7). Increased radiation produced higher rates of photosynthesis and larger stocks of phytoplankton. These phytoplankton stocks in turn supported increased grazing by zooplankton.

Reducing the layer depth produced a slight increase in biomass. Confining the plants in shallower water apparently exposed the phytoplankton stock to higher average radiation intensities and increased algal availability to zooplankton.

Surprisingly, a 10% change in upwelling velocity had negligible effects on plankton biomass. Increasing velocities did produce higher nutrient concentrations (Fig. 9). However, this change in concentration did not yield a similar increase in production. This result stems from the non-linear relationship between nutrient concentration and photosynthetic rate (Fig. 2). Above 1.0 μg-atom/1, changes in nutrient concentration have a small effect on photosynthesis. Since the variations in the simulated nutrient concentrations were observed principally at concentrations above 1.0 μg-atom/1, these fluctuations had a minimal effect on plankton production. The model's response here agrees with Odum's (1971) contention that nutrients are not a limiting factor for phytoplankton production in regions of upwelling.

The largest variation in zooplankton biomass (-65 to +85%) was the result of a ±10% variation in the mixed layer

temperature. Temperature changes directly affect the respiration rate of the zooplankton. Increased temperatures produced higher respiration rates and a net loss of biomass. Conversely, lower temperatures produced lower respiration rates and greater standing stocks. Although the change in daily respiration losses is only slightly affected by temperature (7%/°C @ 15°C), the cumulative affect over a period of months appears significant (see Fig. 10).

VI. DISCUSSION

The primary environmental factor influencing simulated phytoplankton stocks was incident radiation, followed closely by temperature effects (see Table II). The greatest fluctuations in zooplankton biomass resulted from changes in the temperature regime. The response of zooplankton stocks to different thermal conditions suggests a hypothesis concerning the rapid September (warm water period) decrease in zooplankton stocks.

An examination of mixed layer temperatures and predicted upwelling velocities for July and August (Fig. 4) indicate that this period was characterized by a reduction in upwelling (less cold deep water moving towards the surface) which resulted in higher mixed layer temperatures. These higher temperatures may have increased zooplankton respiration sufficiently to produce a net decrease in biomass. In late fall, when lower temperatures returned with algal stocks remaining sufficiently large to permit grazing, a rapid zooplankton increase occurred.

Certainly, other processes contribute to changes in zooplankton stocks. The late summer decline may have been the result of intense predation during this period. Since the model assumes a constant loss to predation and natural mortality, variations in predation have not been considered.

A second possibility is that water masses containing different size plankton stocks may have appeared in Monterey Bay in late summer and winter. The observed changes in the bay have traditionally been described in terms of three oceanographic periods (Skogsberg, 1936; cited in Sverdrup et al., 1942). The "Davidson Current period" (relatively warm water) is normally observed in winter, the "upwelling period" (cold water phase) from early spring through summer, and the "oceanic period" (warm water phase), from late summer through fall. A comparison of these dates with the observed zooplankton fluctuations indicates that the first maximum might be associated with the upwelling period, the minimum with the oceanic, and the second maximum with the Davidson Current period.

Although changing current patterns clearly exist in Monterey Bay, the role of advection in controlling plankton populations may be neglected if (for the time and space scale of interest) the region can be assumed horizontally homogeneous. The total rate of change of a variable "S" as given by the material derivative ($\frac{DS}{Dt}$) is:

$$\frac{DS}{Dt} = \frac{\partial S}{\partial t} + u\,\frac{\partial S}{\partial x} + v\,\frac{\partial S}{\partial y} \qquad (1)$$

The total material derivative ($\frac{DS}{Dt}$) will equal a simple time derivative ($\frac{dS}{dt}$) if the horizontal velocities (u, v) are zero or if the region is horizontally homogeneous, i.e., the spatial derivatives ($\frac{\partial S}{\partial x}$, $\frac{\partial S}{\partial y}$) are zero.

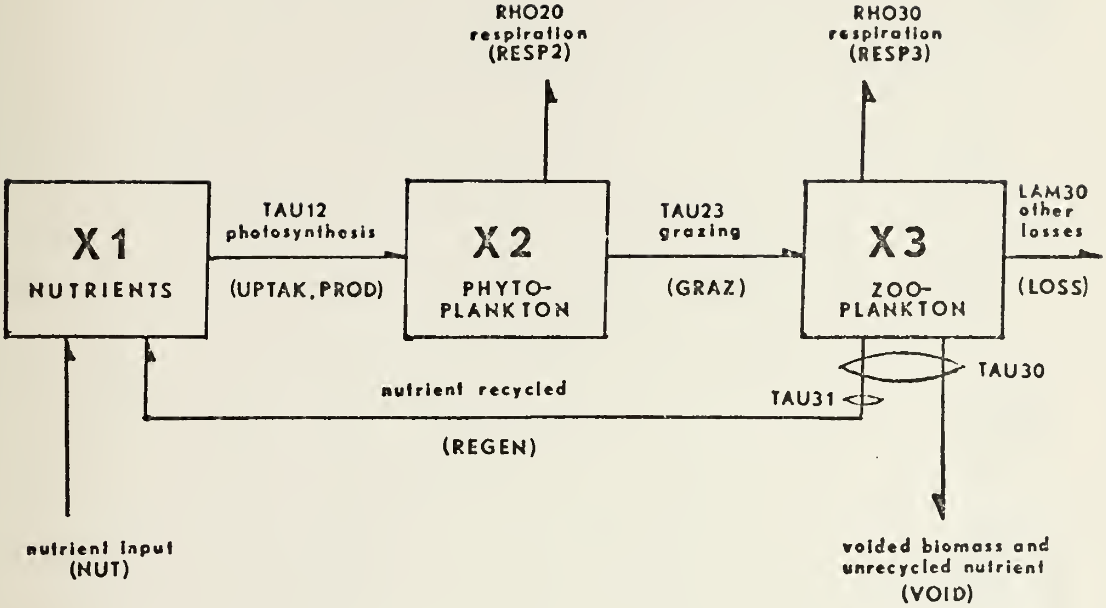
The argument has been made by Bolin and Abbott (1962) that the hydrographic and biological features observed in Monterey Bay are characteristic of a much wider geographic region. These investigators cited evidence that upwelling in the bay is paralleled by upwelling along most of the West Coast of the United States north of Point Conception. Their temperature observations also corroborated closely with the more extensive data reported in CalCOFI Report, VII, 1960. In addition similar phytoplankton observations were made at a station as far distant as La Jolla. Their conclusion was that the assumption of horizontal homogeneity is appropriate for this region.

VII. CONCLUSIONS

The ecosystem model simulated with reasonable accuracy the observed seasonal changes in phosphate concentration and zooplankton biomass. The model inputs used to generate the theoretical results consisted of parameters defining those characteristics of the physical environment which effect biological productivity, e.g., solar radiation, temperature, layer depth, and nutrient input.

Analysis of the model's sensitivity to changes in these environmental parameters identified the possible importance of thermal conditions in regulating the growth of zooplankton populations. These theoretical results suggest a hypothesis related to upwelling. The importance of upwelling as a source of nutrients has long been acknowledged. Simulation results indicate that upwelling may also enhance the growth of zooplankton stocks by bringing colder deep water to the surface thereby reducing zooplankton respiration requirements.

Of course, the model can only suggest the possible significance of this cooling effect. Actual verification of the hypothesis will require a precise knowledge of zooplankton metabolism, as well as additional measurements of phytoplankton and zooplankton biomass. A more detailed simulation study of the effects of upwelling might best be made using a two-dimensional model to analyze variables as a function of depth as well as time.



$$\frac{dX1}{dt} = NUT + REGEN - UPTAK$$

$$\frac{dX2}{dt} = PROD - RESP2 - GRAZ$$

$$\frac{dX3}{dt} = GRAZ - RESP3 - VOID - LOSS$$

FIGURE 1. Ecosystem Compartment Model and Flux Equations.

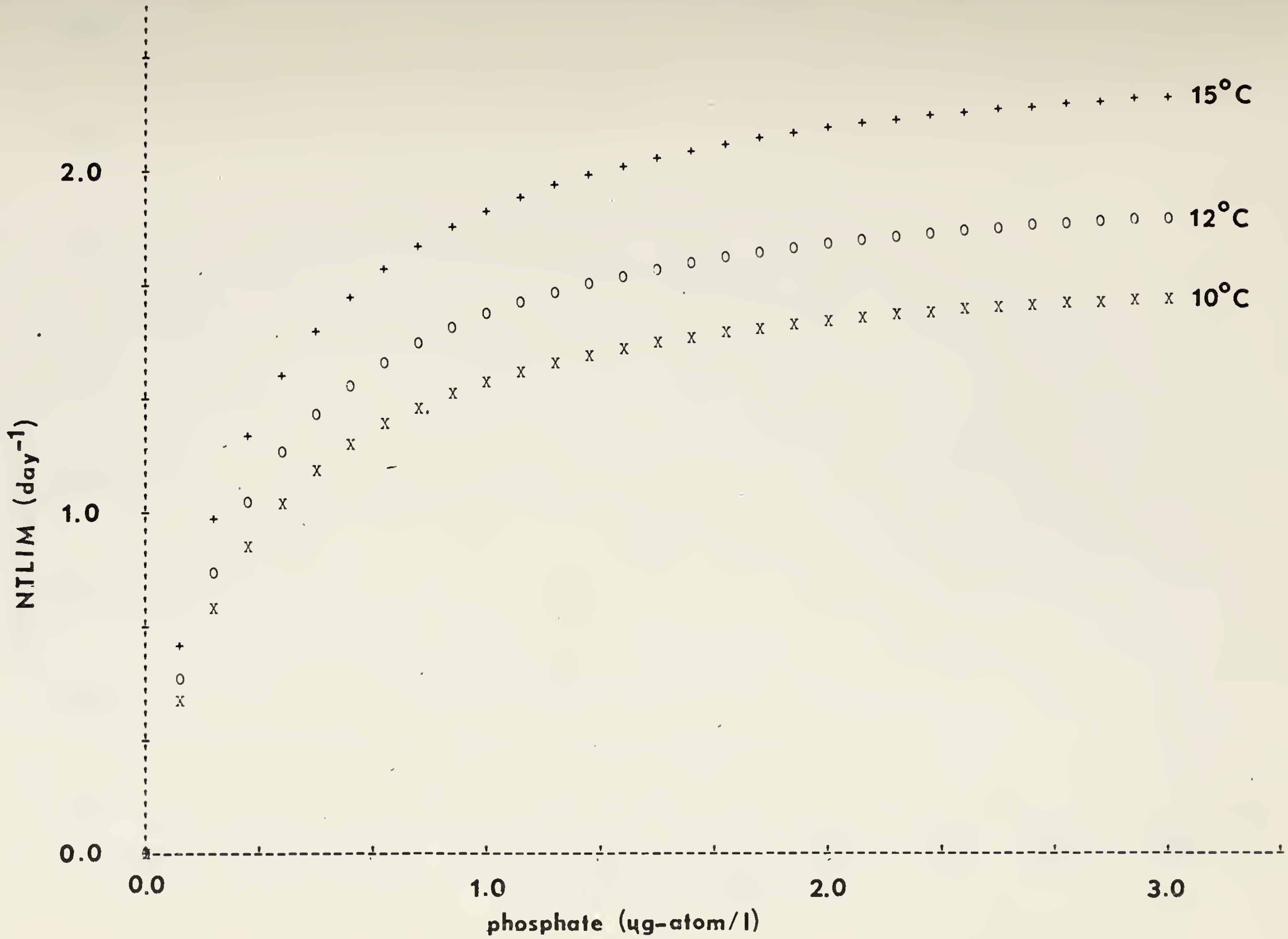


FIGURE 2. Function NTLIM (maximum photosynthetic rate).

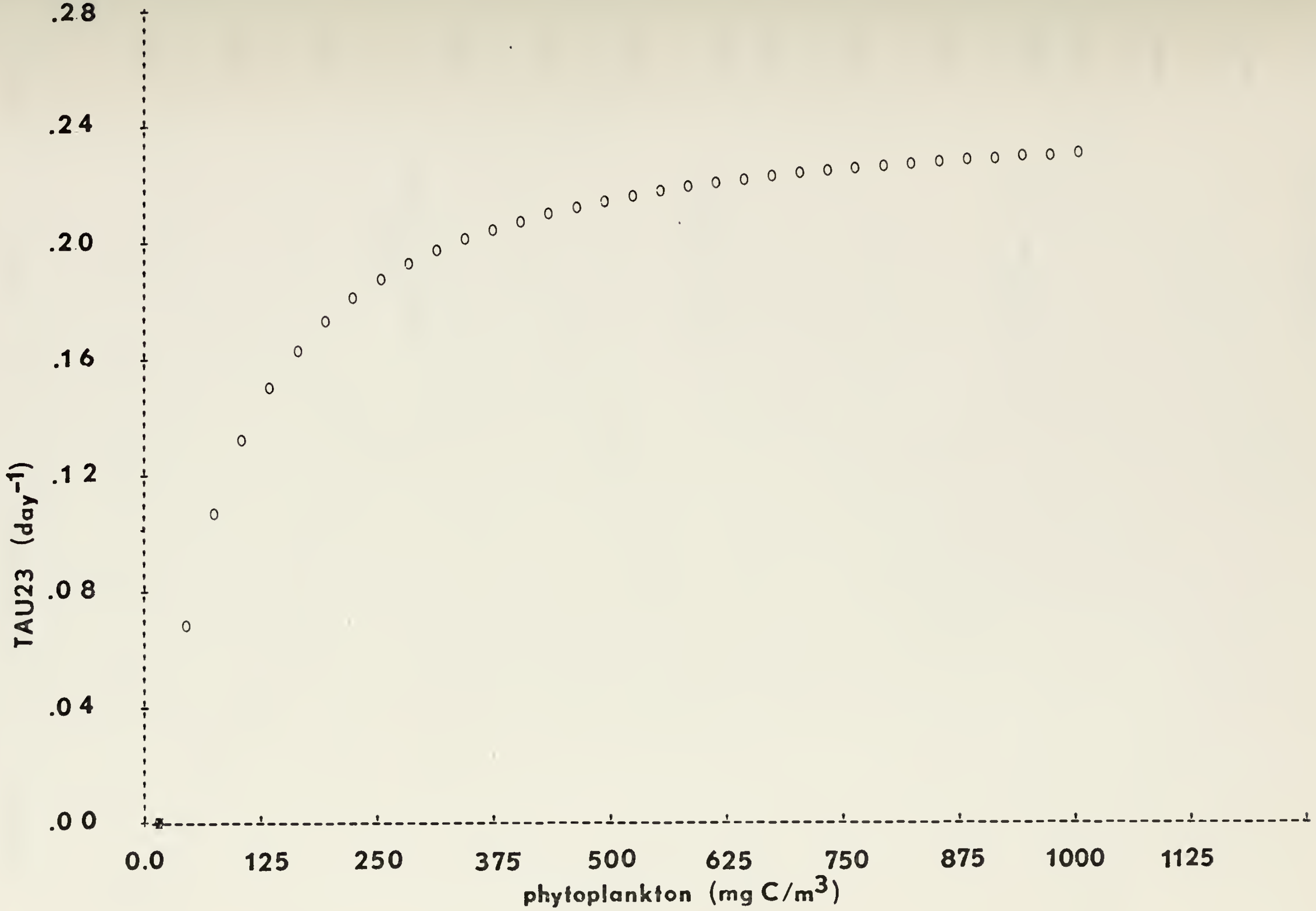


FIGURE 3. Function TAU23 (zooplankton grazing rate).

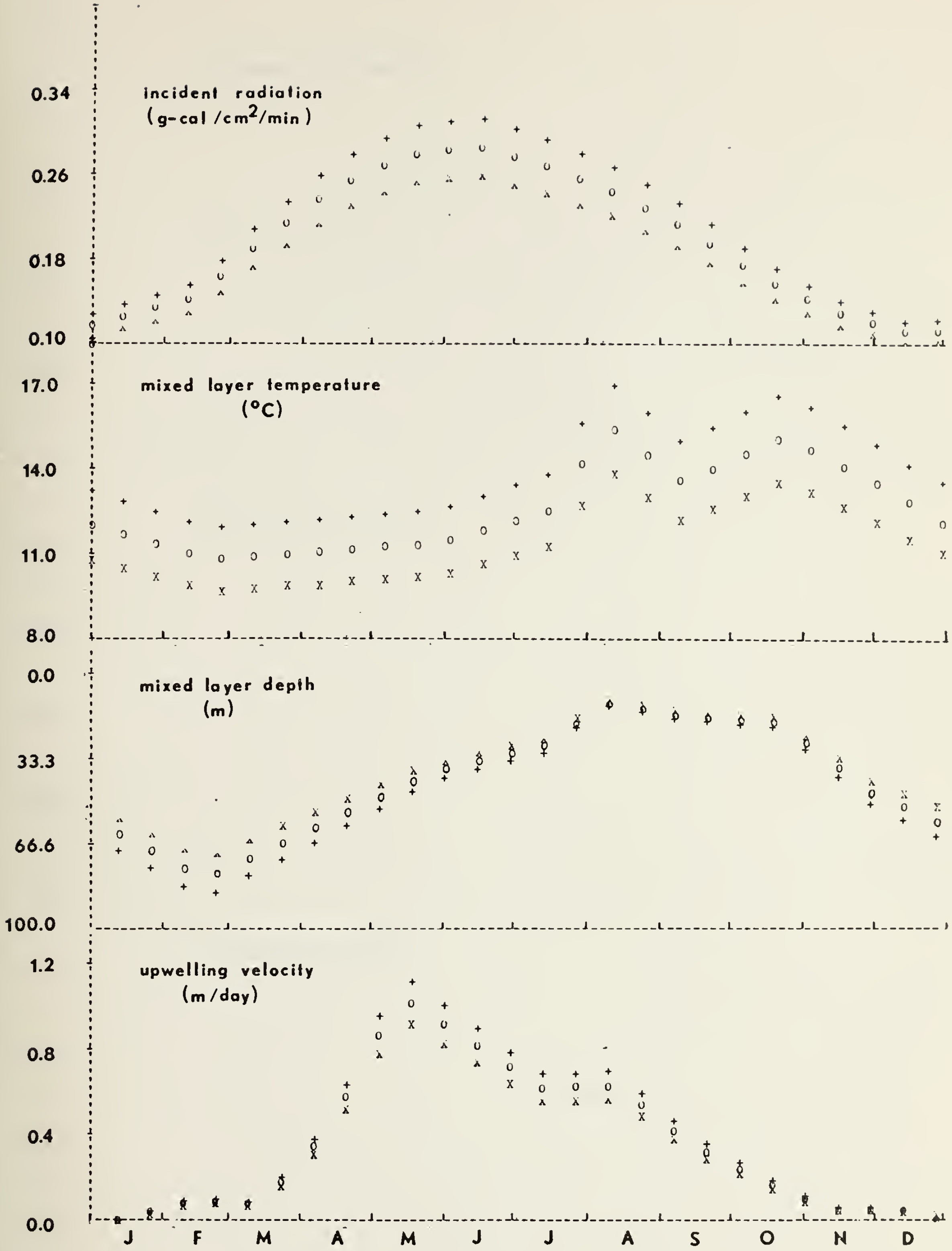


FIGURE 4. Annual Cycle of Environmental Parameters.

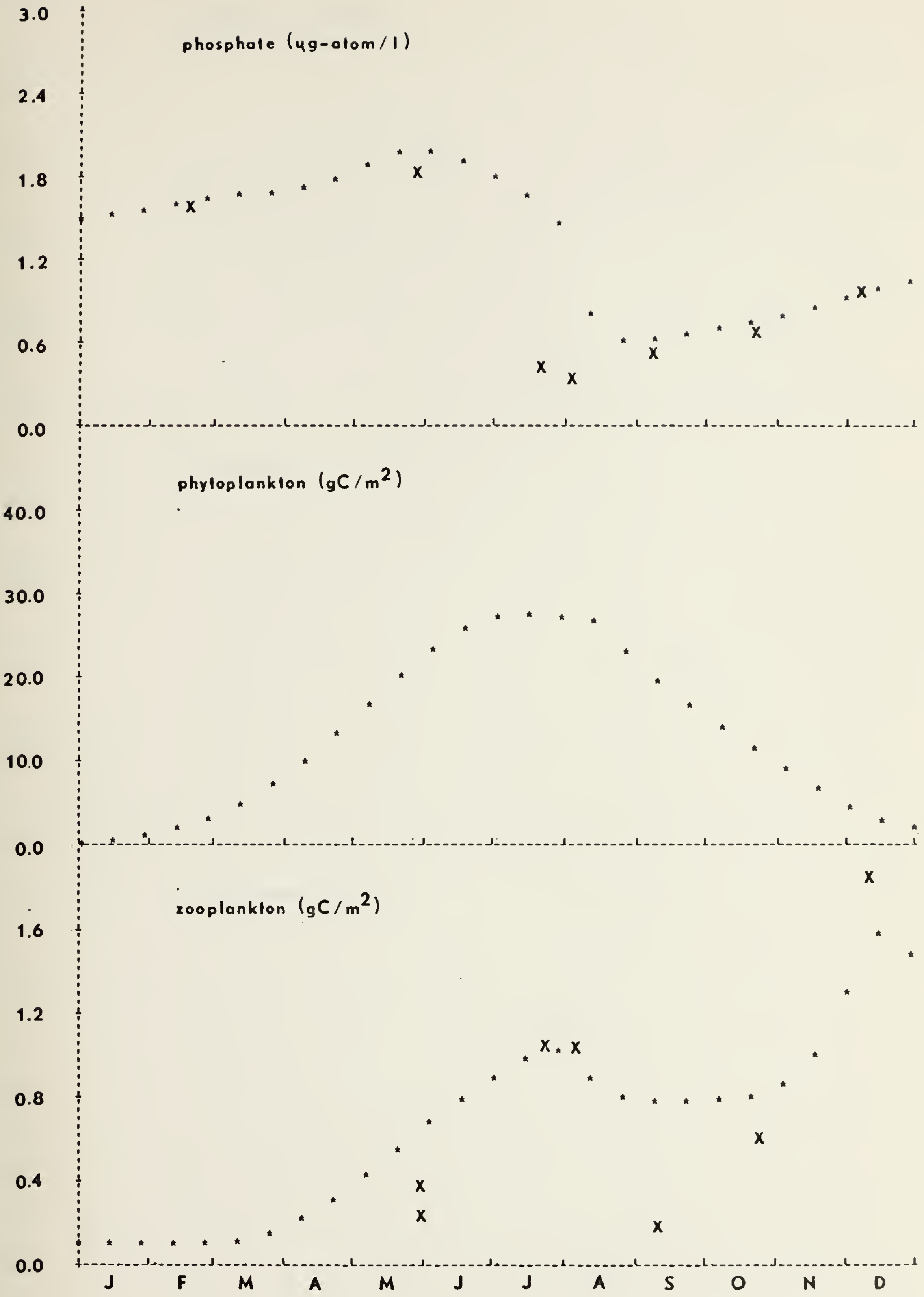


FIGURE 5. Simulation Results (half-saturation constant, KN = 0.6).

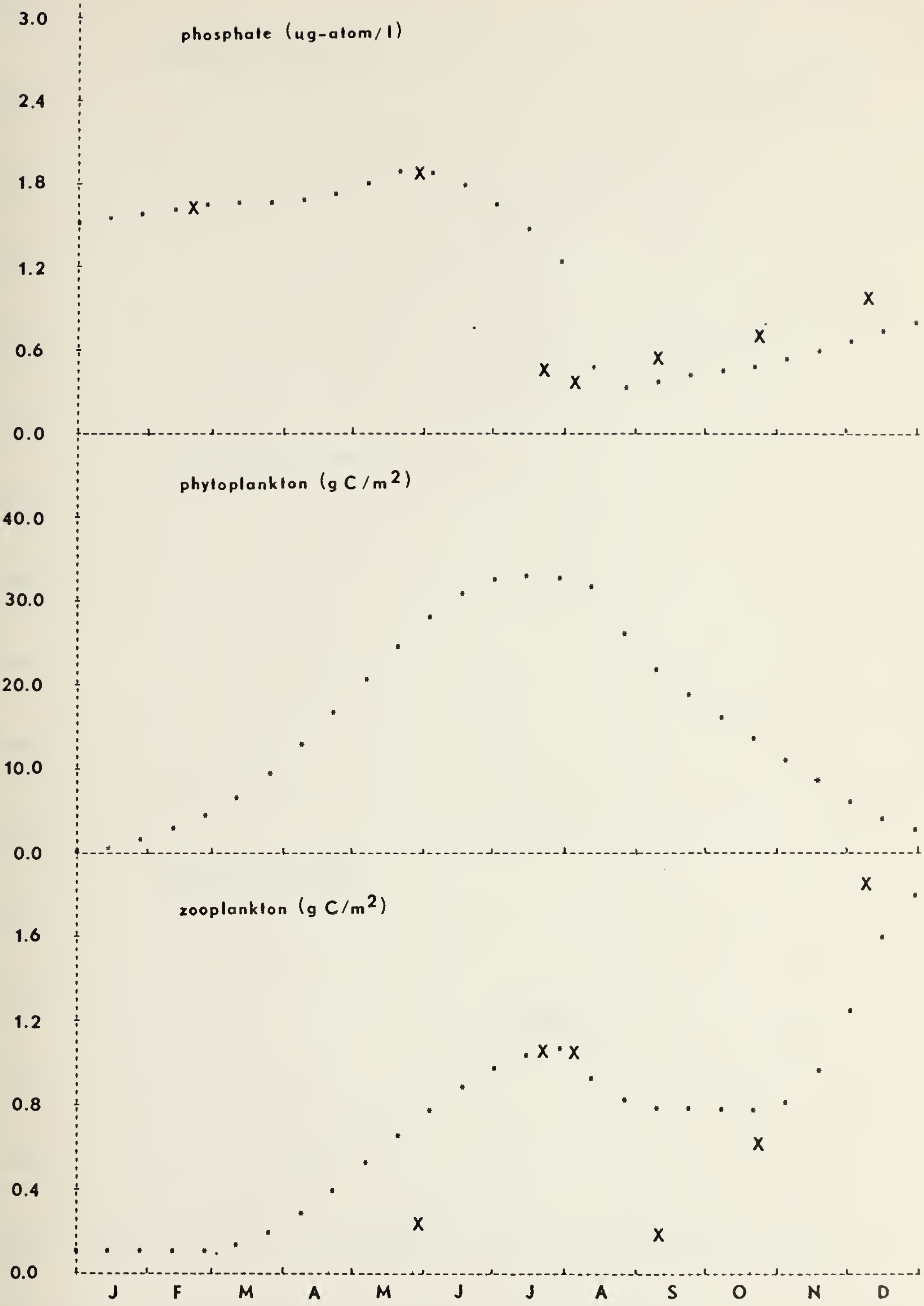


FIGURE 6. Simulation Results (half-saturation constant, KN = 0.3).

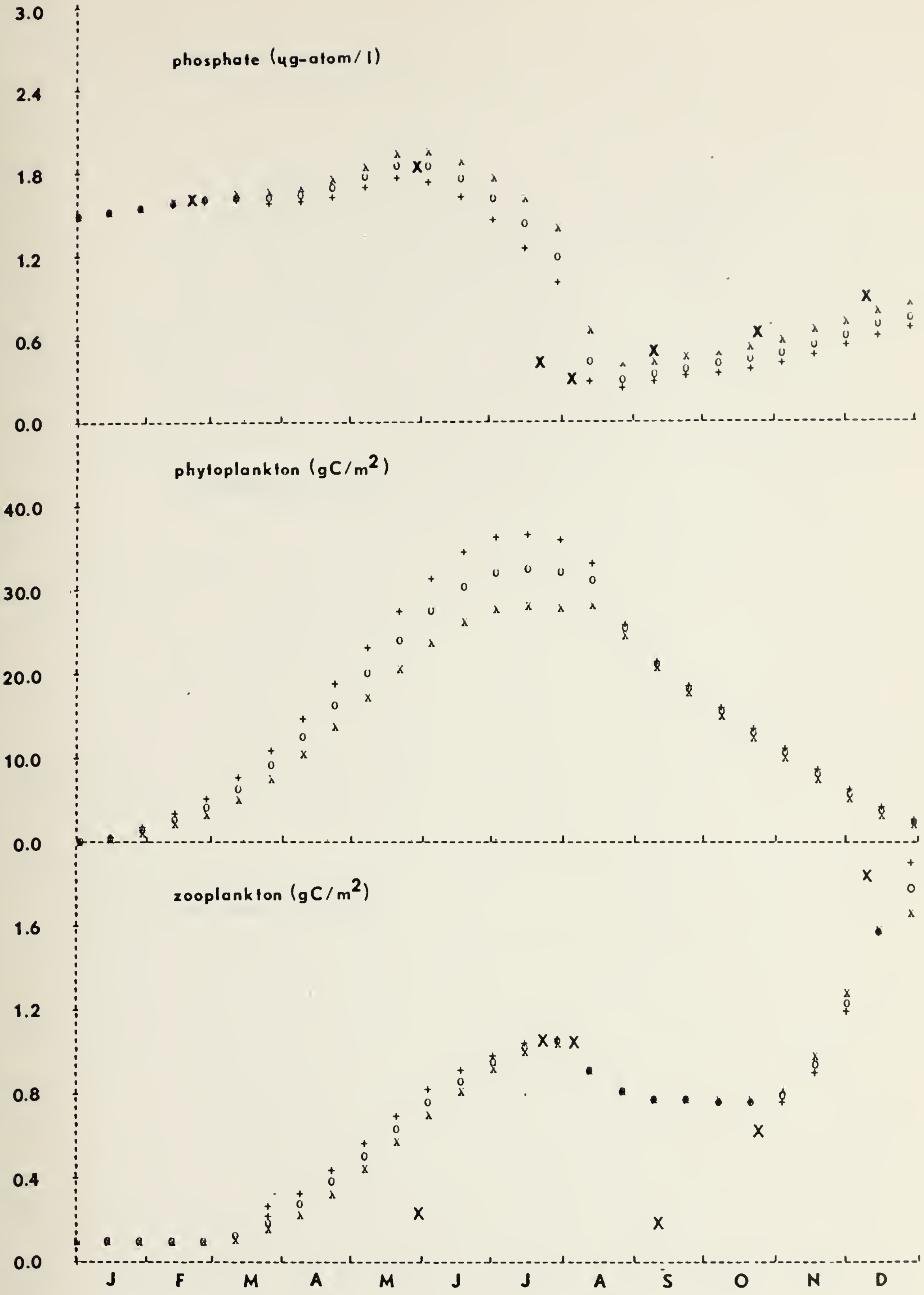


FIGURE 7. Simulation Results (incident radiation, RADI, ±10%).

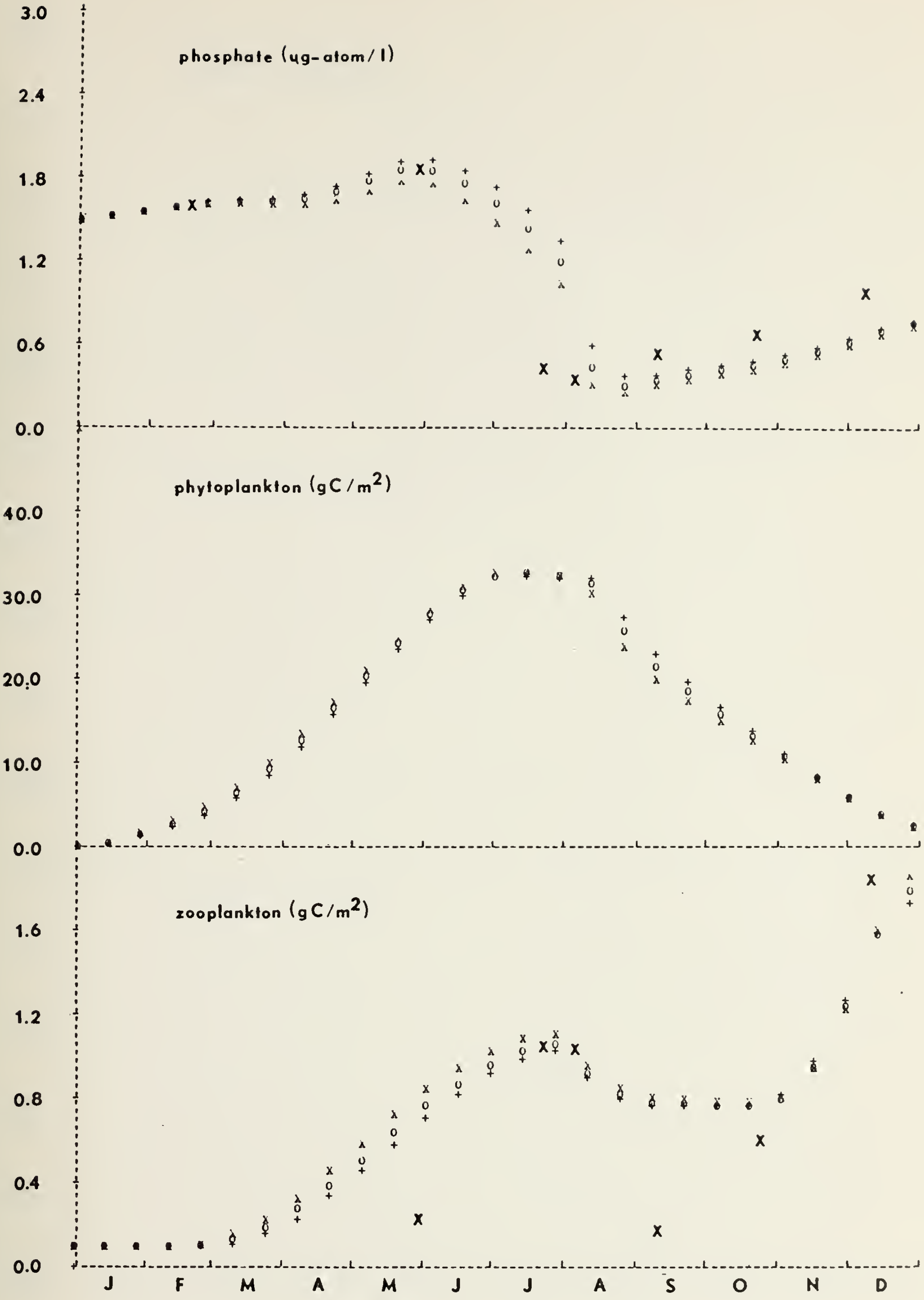


FIGURE 8. Simulation Results (mixed layer depth, Z, ±10%).

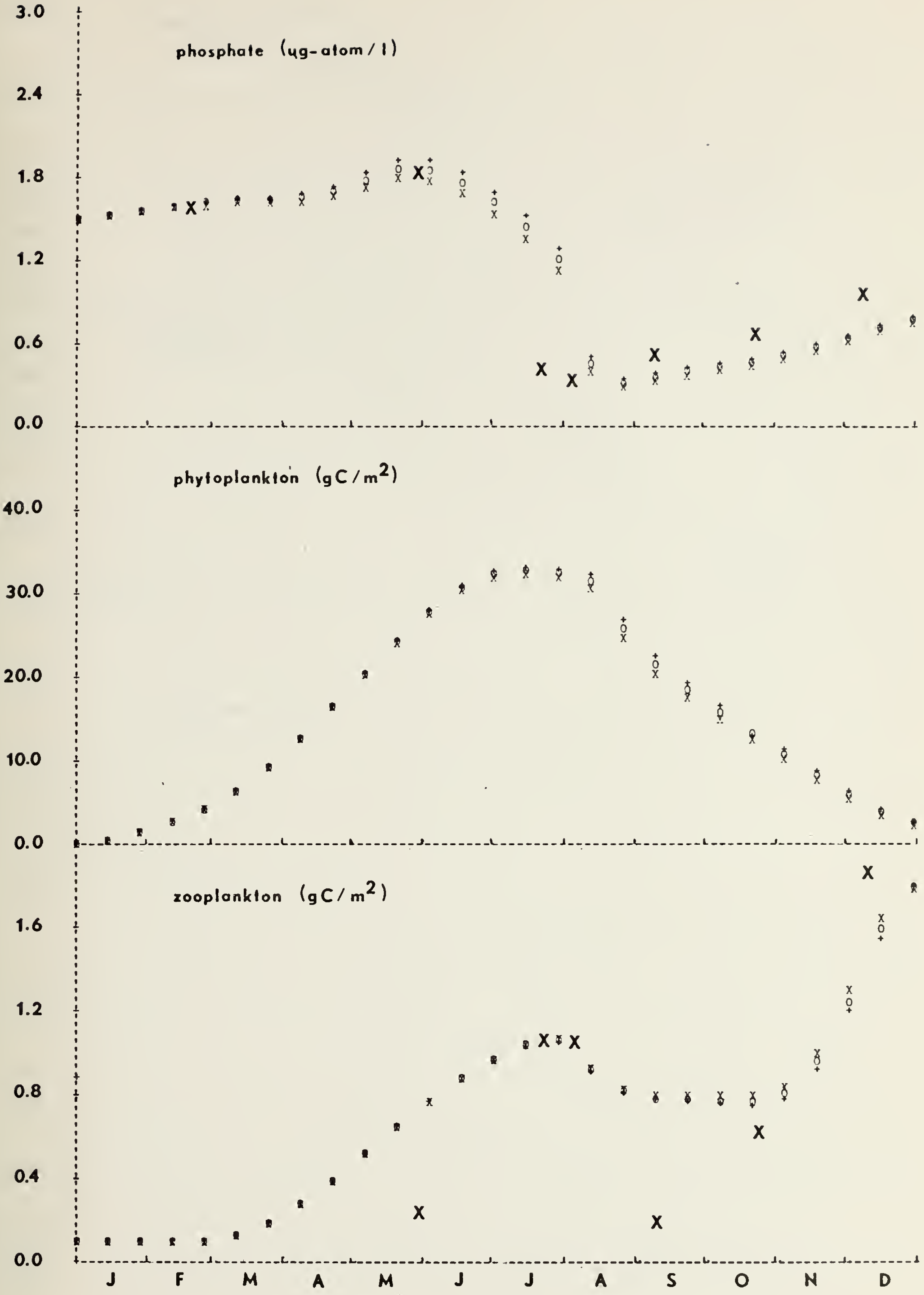


FIGURE 9. Simulation Results (upwelling velocity, W, ±10%).

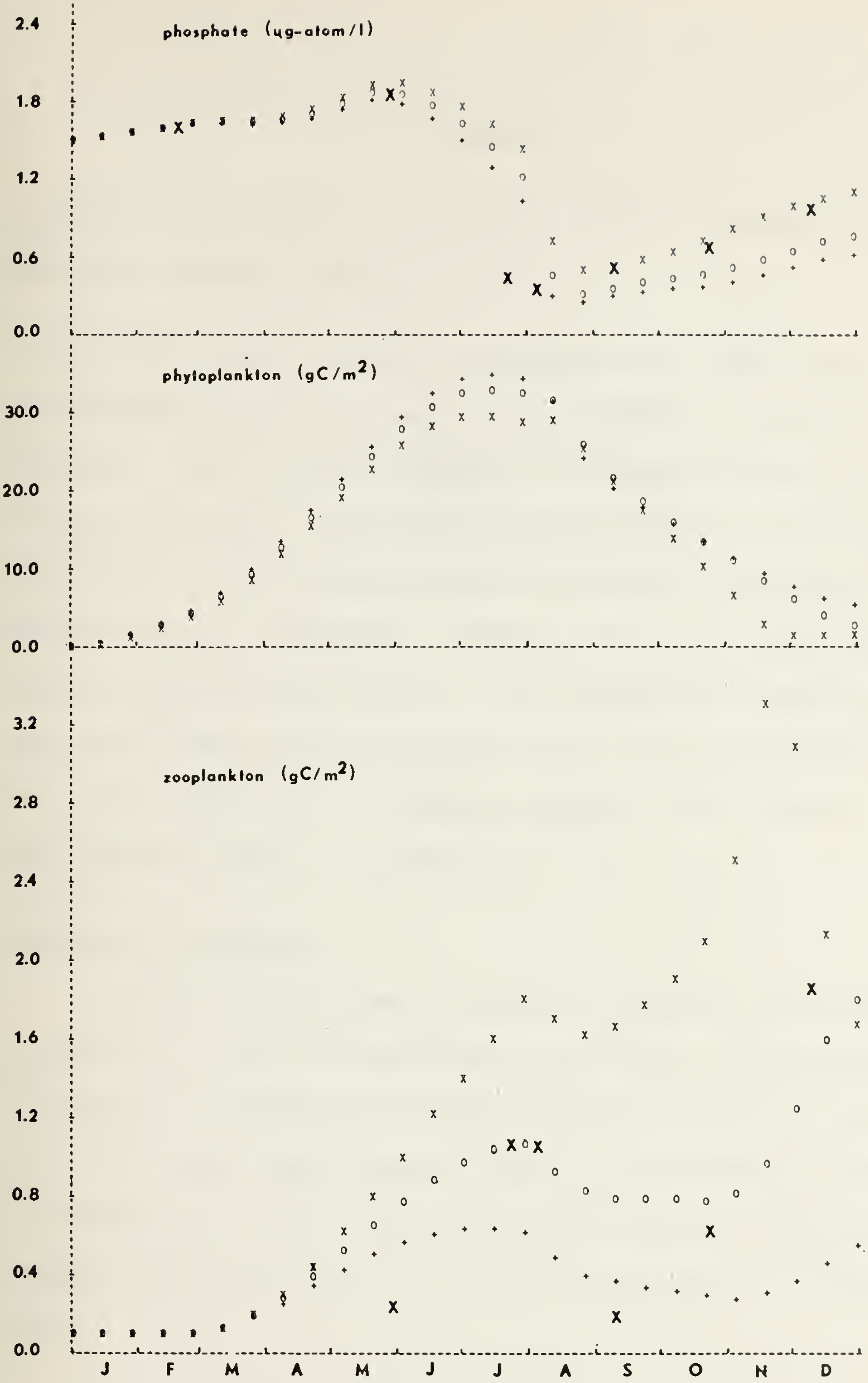


FIGURE 10. Simulation Results (mixed layer temperature, TEMP, ±10%).

APPENDIX A

A BRIEF DESCRIPTION OF THE S/360 CONTIUOUS SIMULATION MODELING PROGRAM (CSMP)

The S/360 CSMP program is devided into three segments, identified by the statement labels INITIAL, DYNAMIC, and TERMINAL. The INITIAL segment is intended for the specification of initial conditions and for defining constants and parameters. The DYNAMIC segment includes the complete description of the system, together with any other computations desired during the run. The TERMINAL segment is used for those computations desired after the completion of each run. The INITIAL and TERMINAL segments are optional, but the DYNAMIC segment is mandatory.

Structure Statements

Structure statements define the model to be simulated. In general, rules for structure statements follow those used in FORTRAN. A library of special CSMP functions is also available. One such function used in the present model is the INTGRL function. This function computes numberically the integral of a function "X." It is expressed in the general form:

Y = INTGRL (IC, X)

where the initial condition is:

```
IC = Y(O).
```

This CSMP statement is equivalent to;

$$Y = \int_{0}^{t} X\,dt + IC$$

Data Statements

Data statements are used to assign numerical values to constants, parameters, and initial conditions. These data cards are specified by the labels CONSTANT, PARAMETER, and INCON respectively. If a specific parameter is to be tested over a range of values a sequence of simulation runs may be designated by enclosing several values of the variable in parentheses. For example;

```
PARAMETER X = (5.0, 5.1, 5.2),
```

specifies three simulation runs. The value of X will be 5.0 in the first run, 5.1 in the second, and 5.2 in the third.

A linear function connecting data points may be specified by the function generator AFGEN. The set of data points is identified using the FUNCTION label:

```
FUNCTION UPWELL = (O., .10), (10., .50).
```

The points are given in sequence, X-coordinate (time) first followed by the y-coordinate. The program connects the data points with a linear function when the AFGEN function is called:

```
W = AFGEN(UPWELL, TIME).
```

Control Statements

Certain operations related to translation, execution, and output segments of the program are specified by special control statements:

INITIAL DYNAMIC TERMINAL	These three labels identify the major segments of the CSMP program.
END	This statement marks the completion of the model's structural description.
SORT NOSORT	These labels determine whether a sequence of cards is to be machine sorted into a correct sequence or executed in the order given.
STOP	This card follows the last END statement in the program.
ENDJOB	This statement denotes the end of a job and must follow the stop card.
TIMER	This label is used with the following CSMP specified variables.
PRDEL	Output print increment.
OUTDEL	Print-plot output print increment.
FINTIM	The maximum time for simulation.

This is only a partial listing of the functions and labels used in the S/360 CSMP language. For a complete description see the IBM User's Manual (1970).

```
// EXEC CSMP360
//CSMP.SYSIN DD *
TITLE    MONTEREY UPWELLING ECOSYSTEM

***********************************************************************
***********************************************************************
** THIS MODEL SIMULATES THE SEASONAL FLUCTUATIONS IN THREE STATE     **
** VARIABLES- MIXED LAYER PHOSPHATE CONCENTRATION (X1), PHYTOPLANKTON**
** BIOMASS (X2), AND HERBIVOROUS ZOOPLANKTON BIOMASS (X3).  THE      **
** SIMULATION RESULTS ARE DEPENDENT ON ANNUAL VARIATIONS IN FOUR     **
** ENVIRONMENTAL PARAMETERS THAT INFLUENCE BIOLOGICAL PRODUCTIVITY   **
** IN A REGION OF UPWELLING.  THE PARAMETERS INCLUDE INCIDENT RADI-  **
** ATION (RADI),  UPWELLING VELOCITY (W), MIXED LAYER TEMPERATURE    **
** (TEMP), AND MIXED LAYER DEPTH (Z).                                **
***********************************************************************
***********************************************************************

***********************************************************************
** THE INITIAL SEGMENT CONTAINS MUMERICAL VALUES FOR INITIAL         **
** CONDITIONS, CONSTANTS, AND PARAMETERS.                            **
***********************************************************************

INITIAL

      INCON IC1=1.5, IC2=0.1, IC3=0.1

      CONSTANT B=0.5, C=0.774, DX1=3.0, EKL=50.0, FAVL=0.8, KG=80.0,...
      KN=0.6, L=0.01, M=0.12, MAXG=0.25, P=2.5, R=0.069,...
      RHOZ2=0.0175, RHOZ3=0.019, S=0.13,  X1MIN=0.0, X2MIN=16.0,...

      WFAC=0.17, ZFAC=1.0, TFAC=1.0, RFAC=1.0

      PARAMETER WFAC=(.153, .170, .187)

DYNAMIC

***********************************************************************
** ENVIRONMENTAL FUNCTIONS ARE DEFINED BY THE LINEAR FUNCTION        **
** GENERATOR, AFGEN.                                                 **
***********************************************************************

      FUNCTION SOLAR=(00.,.123), (46.,.158), (74.,.224),...
      (105.,.286), (135.,.324), (166.,.335), (196.,.311),...
      (227.,.278), (258.,.235), (288.,.181), (319.,.141),...
      (349.,.117), (365.,.119)
      RCOMP=AFGEN(SOLAR, TIME)
```

```
      FUNCTION UPWELL=(0.,0.), (15.,0.), (45.,.57), (75.,.48), ...
      (105.,2.56), (135.,6.24), (165.,4.98), (195.,3.68), ...
      (227.,3.75), (258.,2.21), (288.,1.19), (319.,.33),...
      (349.,.33), (365.,.0)
      WCOMP=AFGEN(UPWELL,TIME)

      FUNCTION STEMP=(0.,12.0),(51.,10.8),(150.,11.4),(204.,12.7),...
      (217.,15.8),(253.,13.5),(297.,15.1),(344.,13.1),(365.,12.0)
      TCOMP=AFGEN(STEMP, TIME)

      FUNCTION LAYER=(0.,70.),(51.,100.),(150.,47.),(204.,33.),...
      (217.,13.),(253.,20.),(297.,24.),(344.,65.),(365.,70.)
      ZCOMP=AFGEN(LAYER,TIME)

**********************************************************************
** VARIATIONS IN ENVIRONMENTAL PARAMETERS ARE GENERATED BY          **
** MULTIPLYING THE COMPUTED VALUE BY A CONSTANT FACTOR, I.E., WFAC, **
** ZFAC, ETC.                                                       **
**********************************************************************

      RADI=RFAC*RCOMP

      W=WFAC*WCOMP

      TEMP=TFAC*TCOMP

      Z=ZFAC*ZCOMP

**********************************************************************
** NEXT, VARIABLES REQUIRED IN RATE EQUATIONS ARE CALCULATED.       **
**********************************************************************

      MAXN=S*TEMP+B

      NTLIM=MAXN*(X1-X1MIN)/(KN+(X1-X1MIN))

      CL=33.333*(X2/Z)

      K=0.04+0.0088*CL+0.054*CL**0.666666

      X2MG=1000.*(X2/Z)

      UPWEL=(W/EKL)*(DX1-X1)

      MIX=(M/Z)*(DX1-X1)

      RAD=RADI/(K*Z)*(1.0-EXP(-K*Z))
```

```
***********************************************************************
** RATE EQUATIONS ARE COMPUTED.                                      **
***********************************************************************

      TAU12=P*RAD*NTLIM

      TAU23= MAXG*(X2MG-X2MIN)/(KG+(X2MG-X2MIN))

      NOSORT
      IF(TAU23.LT.0.0) TAU23=0.0
      SORT

      TAU30=(0.8*(TAU23/MAXG))*TAU23

      TAU31=FAVL*(C/Z)*TAU30

      RHO20=RHOZ2*EXP(R*TEMP)

      RHO30=RHOZ3*EXP(R*TEMP)

      LAM30=L

***********************************************************************
** FLUXES ARE COMPUTED FROM RATE EQUATIONS.                          **
***********************************************************************

      NUT=UPWEL+MIX

      REGEN=TAU31*X3

      UPTAK=C*TAU12*(X2/Z)

      PROD=TAU12*X2

      RESP2=RHO20*X2

      GRAZ=TAU23*X3

      RESP3=RHO30*X3

      VOID=TAU30*X3

      LOSS=LAM30*X3
```

```
***********************************************************************
** CHANGES IN THE STATE VARIABLES ARE COMPUTED AS THE SUM OF FLUXES. **
***********************************************************************

      X1DOT=NUT+REGEN-UPTAK

      X2DOT=PROD-RESP2-GRAZ

      X3DOT=GRAZ-RESP3-VOID-LOSS

***********************************************************************
** FINALLY, THE NEW VALUES FOR THE STATE VARIABLES ARE COMPUTED.     **
***********************************************************************

      X1=INTGRL(IC1,X1DOT)

      X2=INTGRL(IC2,X2DOT)

      X3=INTGRL(IC3,X3DOT)

      NOSORT
      IF(X3.LT.0.1) X3=0.1

      TIMER FINTIM=364.,  OUTDEL=14.0

      PRTPLOT X1(NUT, REGEN, UPTAK)
      PRTPLOT X2(PROD,  RESP2, GRAZ)
      PRTPLOT X3(GRAZ, RESP3, VOID)
      END
      STOP
ENDJOB
```

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